The "pseudofirmisternal" pectoral girdle of anurans

Moises KAPLAN

Division of reptiles and amphibians, Museum of Zoology, University of Michigan, Ann Arbor, MI 48109, USA
<moiseska@umich.edu>

The pectoral girdles of the following species were studied histologically: (1) Brachycephalidae: *Brachycephalus ephippium*; (2) Bufonidae: *Atelopus subornatus*, *Frostius pernambucensis*, *Osornophryne bufoniformis*; (3) Leptodactylidae: *Geobatrachus walkeri*, *Insuetophrynus acarpicus*; (4) Pipidae: *Hymenochirus boettgeri*; (5) Ranidae: *Rana sylvatica*; (6) Rhinodermatidae: *Rhinoderma darwinii*. Of the non-ranoid frogs, only *A. subornatus*, *F. permanbucensis*, *H. boettgeri* and *O. bufoniformis* have completely fused, non-overlapping, epicoracoids (i.e., pseudofirmisterny). The girdle morphologies of *G. walkeri* and *R. darwinii* are unique in anurans. The girdles of *B. ephippium* and *I. acarpicus* are arciferofirmisternal. Morphological differences between the pseudofirmisternal and firmisternal girdles suggest they are not homologous.

INTRODUCTION

Pseudofirmisterny is the term describing the pectoral girdles of frogs, other than Ranoidea (i.e., Dendrobatidae, Hyperoliidae, Microhylidae, Ranidae and Rhacophoridae sensu FORD & CANNATELLA, 1993, or Hyperoliidae, Microhylidae, Ranidae, Mantellidae and Rhacophoridae sensu VENCES & GLAW, 2001), having the epicoracoid cartilages completely fused to (i.e., from anterior to posterior) and not overlapping one another.

The following genera of non-ranoid frogs are considered to have pseudofirmisternal girdles: *Brachycephalus* (including *Psyllophryne*, KAPLAN, 2002), *Atelopus*, *Frostius*, *Osornophryne*, *Atopophrynus*, *Geobatrachus*, *Insuetophrynus*, *Hymenochirus*, *Pseudhymenochirus* and *Rhinoderma* (BARRIO, 1970, TRUEB, 1973; RUIZ-CARRANZA & HERNANDEZ-CAMACHO, 1976, LYNCH, 1978, ARDILLA-ROBAYO, 1979; LYNCH & RUIZ-CARRANZA, 1982, CANNATELLA, 1985, 1986; DUELLMAN & TRUEB, 1985, MYERS & FORD, 1986, CANNATELLA & TRUEB, 1988; GRAYBEAL, 1997, however, see MCLACHLAN, 1943, GRIFFITHS, 1957, 1963; MCDIARMID, 1969). The non-ranoid, pseudofirmisternal family Dendrobatidae (LYNCH, 1973, HAY et al., 1995, FELLER & HEDGES, 1998, VENCES & GLAW, 2000, 2001) was not examined. The above distribution of pseudofirmisterny in anurans is questionable, because only the girdles of *Brachycephalus ephippium* and *Rhinoderma darwinii* have been examined histologically and

observations of the pectoral girdle in cleared-and-stained specimens frequently are misleading (KAPLAN, 1993).

Generally, it is accepted that the character "epicoracoids completely fused and not overlapping one another" evolved independently in both non-ranoid and ranoid anurans (NOBLE, 1926; GRIFFITHS, 1963, DUELLMAN & TRUEB, 1985; FORD & CANNATELLA, 1993). Moreover, it is thought that this character evolved several times in non-ranoid frogs – viz., in *Insuetophrynus*, *Rhinoderma* and *Brachycephalus* (GRIFFITHS, 1963; LYNCH, 1978, DUELLMAN & TRUEB, 1985; FORD & CANNATELLA, 1993), in the ancestors of *Frostius*, *Atelopus* and *Osornophryne* (CANNATELLA, 1986; GRAYBEAL, 1997), in *Hymenochirus* and *Pseudhymenochirus* (CANNATELLA & TRUEB, 1988), and in *Atopophrynus* and *Geobatrachus* (MYERS & FORD, 1986). However, it is still unclear if these hypotheses are parsimonious, because there is no available cladistic analysis of the taxa with this girdle morphology. The character pseudofirmisterny supported the following monophyletic groups: *Brachycephalus* and *Atelopus* (GRIFFITHS, 1963), *Brachycephalus* and *Psyllophryne* (FORD & CANNATELLA, 1993), *Atelopus*, *Frostius* and *Osornophryne* (CANNATELLA, 1986; GRAYBEAL, 1997), and *Geobatrachus* and *Atopophrynus* (MYERS & FORD, 1986).

Herein, I describe the ventromedial parts of the pectoral girdles of most frogs that have been described as pseudofirmisternal, along with one having a firmisternal girdle – i.e., the pectoral girdles of ranoid frogs having the epicoracoids completely fused (FORD & CANNATELLA, 1993). The descriptions are based on examination of serial sections which were prepared to determine, first, whether the examined frogs have the epicoracoids completely fused and not overlapping, and second, whether the hypothesis that pseudofirmisterny evolved several times from firmisterny is consistent with the morphology (i.e., anatomical differences between non-ranoid and ranoid frogs). The systematic implications of these observations will be discussed

MATERIALS AND METHODS

The midventral parts of the breast shoulder apparatus of sexually mature individuals of the following families and species of frogs were sectioned: (1) Brachycephalidae *Brachycephalus ephippium* (UMMZ 103568), (2) Bufonidae *Atelopus subornatus* (ICN 15820), *Frostius pernambucensis* (UMMZ 225143), *Osornophryne bufoniformis* (ICN 11505), (3) Leptodactylidae *Geobatrachus walkeri* (ICN 35186), *Insuetophrynus acarpicus* (UMMZ 225142); (4) Pipidae *Hymenochirus boettgeri* (UMMZ 229751), (5) Ranidae, *Rana sylvatica* (UMMZ 229752); (6) Rhinodermatidae *Rhinoderma darwinii* (UMMZ 143361). The medial part of the breast-shoulder apparatus was excised by cutting through the procoracoid cartilages, clavicles and coracoid bones; the epicoracoids and the attached prezonal and postzonal elements were removed, decalcified (Cal-Ex II, Fisher Scientific), embedded in paraffin (WEISSNER, 1960), sectioned transversely from the anterior tip of the omosternum to the posterior tip of the sternum, and stained with hematoxylin and eosin.

The names of the muscles of *Atelopus subornatus*, *Brachycephalus ephippium*, *Hymenochirus boettgeri*, *Rana sylvatica* and *Rhinoderma darwinii* follow those in TYSON's (1987) and

BEDDARD's (1895, 1908) studies. The muscles of *Osornophryne bufoniformis*, *Frostius pernambucensis*, *Insuetophrynus acarpicus* and *Geobatrachus walkeri* are designated by numbers, as myological studies of these taxa are not available. Histological terminology follows that of FAWCETT (1986). Drawings of the girdles of *Atelopus farci* (KAPLAN, 1994) and *Pseudhymenochirus curtipes* (DE VILLIERS, 1929) are used instead of those of *A. subornatus* and *H. boettgeri* because the latter are not available.

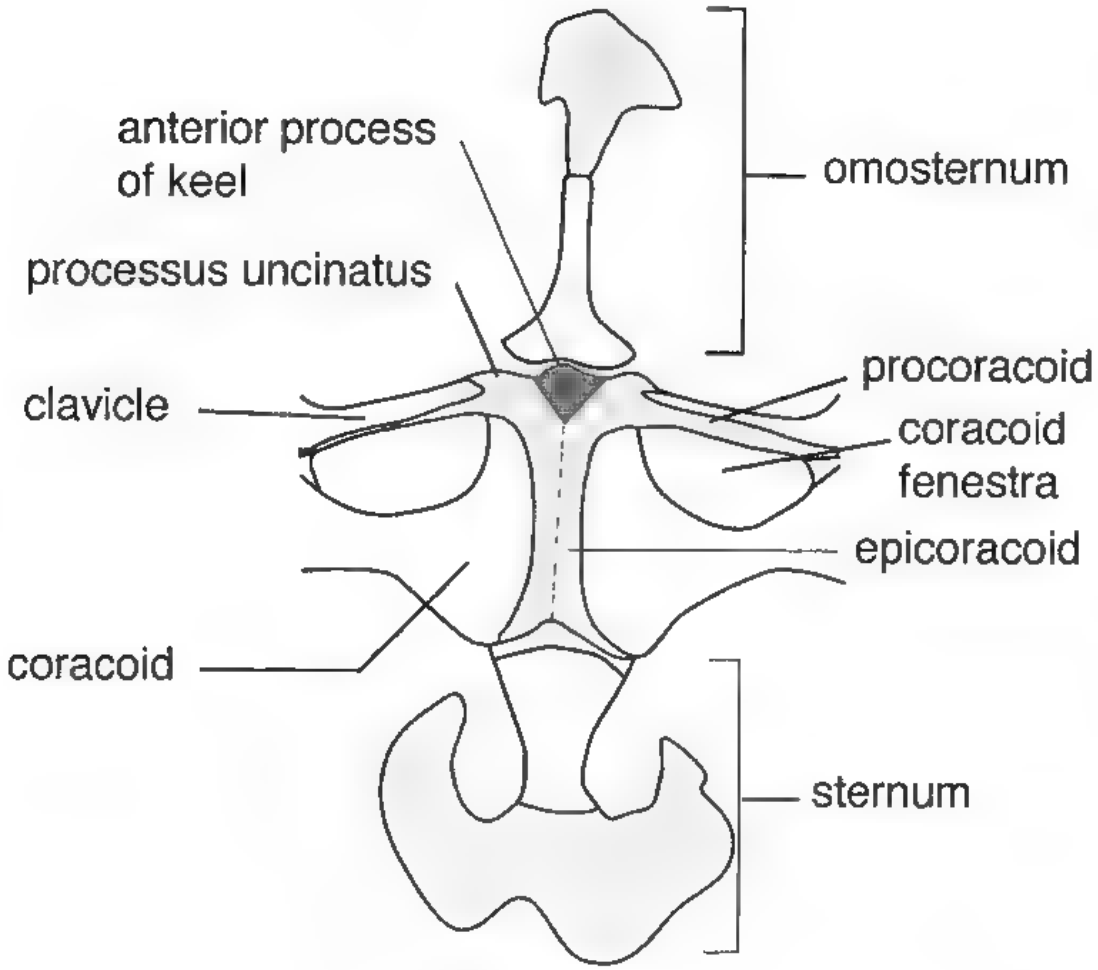
Herein, I consider the epicoracoid cartilages to be the ventromedial elements of the girdle extending from the level of the clavicles to the coracoids, including the parts lying medial to the procoracoid shafts (GRIFFITHS, 1963; but see TYSON, 1987 and DUELLMAN & TRUEB, 1985) and the coracoid bones (i.e., the ossified portion of the embryonic coracoid-epicoracoid cartilage TYSON, 1987, KAPLAN, 1993), and anterior to the clavicles (fig. 1); note that the medial position of the epicoracoids with respect to the procoracoid is assumed because they are indistinguishably fused in sexually mature individuals. I consider the epicoracoid horns to be the part of the epicoracoid cartilages that lie posterior to the posteromedial part of the coracoids. "Medial ligament" refers to the band of dense connective tissue ventromedial to the epicoracoids. The term "completely fused" refers to the fusion of the epicoracoids from their anterior to posterior tips. The term "fused" describes epicoracoids whose medial ends, or part of them, are united synchondrotically or by connective tissue that changes gradually from cartilage, near the epicoracoids, to dense regular connective tissue, at the midline. "Indistinguishably fused" is used to describe absence of a suture between the epicoracoids, where "suture" is defined as a thin, transverse band of cartilage with low cell, and high fiber, densities, different coloration, and/or refrective properties. The epicoracoids are considered "overlapping" when every part of their medial ends are aligned with one another on the vertical axis. The descriptors "left" and "right" refer to the organism's left and right sides from the dorsal perspective.

Developmental stages are given according to GOSNER (1960). The following abbreviations are used to designate the collections where the specimens studied are kept: ICN, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogota, Colombia; UMMZ, University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA.

RESULTS

BRACHYCEPHALUS EPHIPPIUM

Anteriorly (fig. 2, 3A), the epicoracoids (e) are fused indistinguishably to one another on the midline at the level of the clavicle (cl). Slightly posterior (fig. 3B), there is a suture (su) between the epicoracoids. Posteriorly (fig. 3C), the epicoracoids are marked by a shallow dorsomedial crevice (cr) and a broad ventromedial keel (k), loose regular connective tissue fills the crevice. The *m. supracoracoideus* (msc) inserts on the ventral keel, medial ligament (ml) and ventral surfaces of the procoracoids (p). Posterior to the procoracoids (fig. 3D), two flat, expanded coracoids (co) flank the epicoracoids; the medial end of each coracoid has a cartilaginous core, that is indistinguishable from the epicoracoids, surrounded by a bony layer. Posteriorly (fig. 3E), the epicoracoids are free, the left side of the ventral keel is replaced



Rana sylvatica

Fig. 1. – The ventral elements of the pectoral girdle of *Rana sylvatica* (adapted from TYSON, 1987) Dashed mid line: medial edge of epicoracoids; light gray: cartilage; dark gray: loose connective tissue; white: bone.

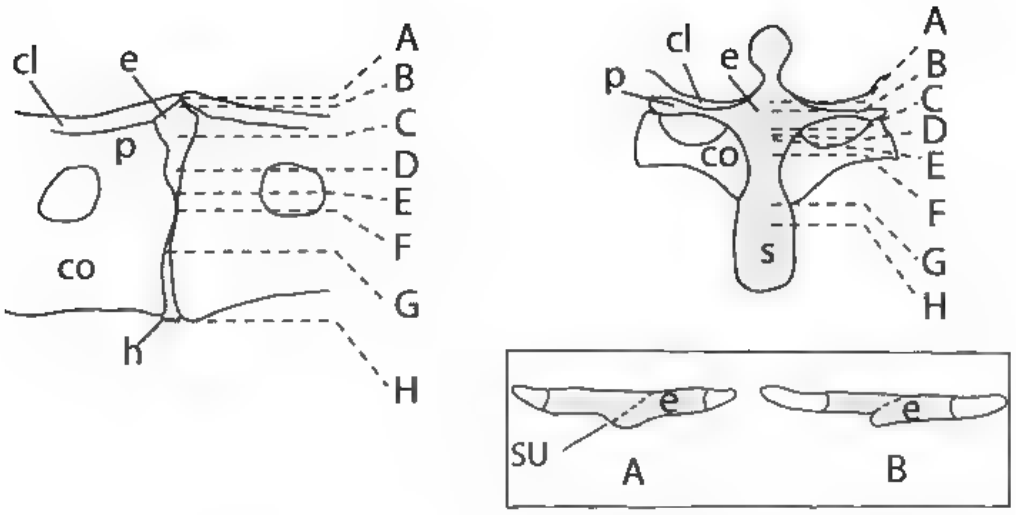


Fig. 2 Ventral view of the pectoral girdle of *Brachycephalus ephippium* (adapted from TYSON, 1987), *Rhinoderma darwinii* (adapted from CEI, 1980), *Insuetophrynus acarpicus* (adapted from BARRIO, 1970) and *Geobatrachus walkeri* (adapted from ARDILLA-ROBAYO, 1979). cl, clavicle; co, coracoid e epicoracoid, h, epicoracoid horn; p, procoracoid; s, sternum; su, suture. White: bone; light gray cartilage; dark gray: area where the coracoids and epicoracoids are desorganized. A-H transverse sections corresponding to those of fig 3-6. A and B in insert: transverse sections corresponding to those of fig. 4D-E

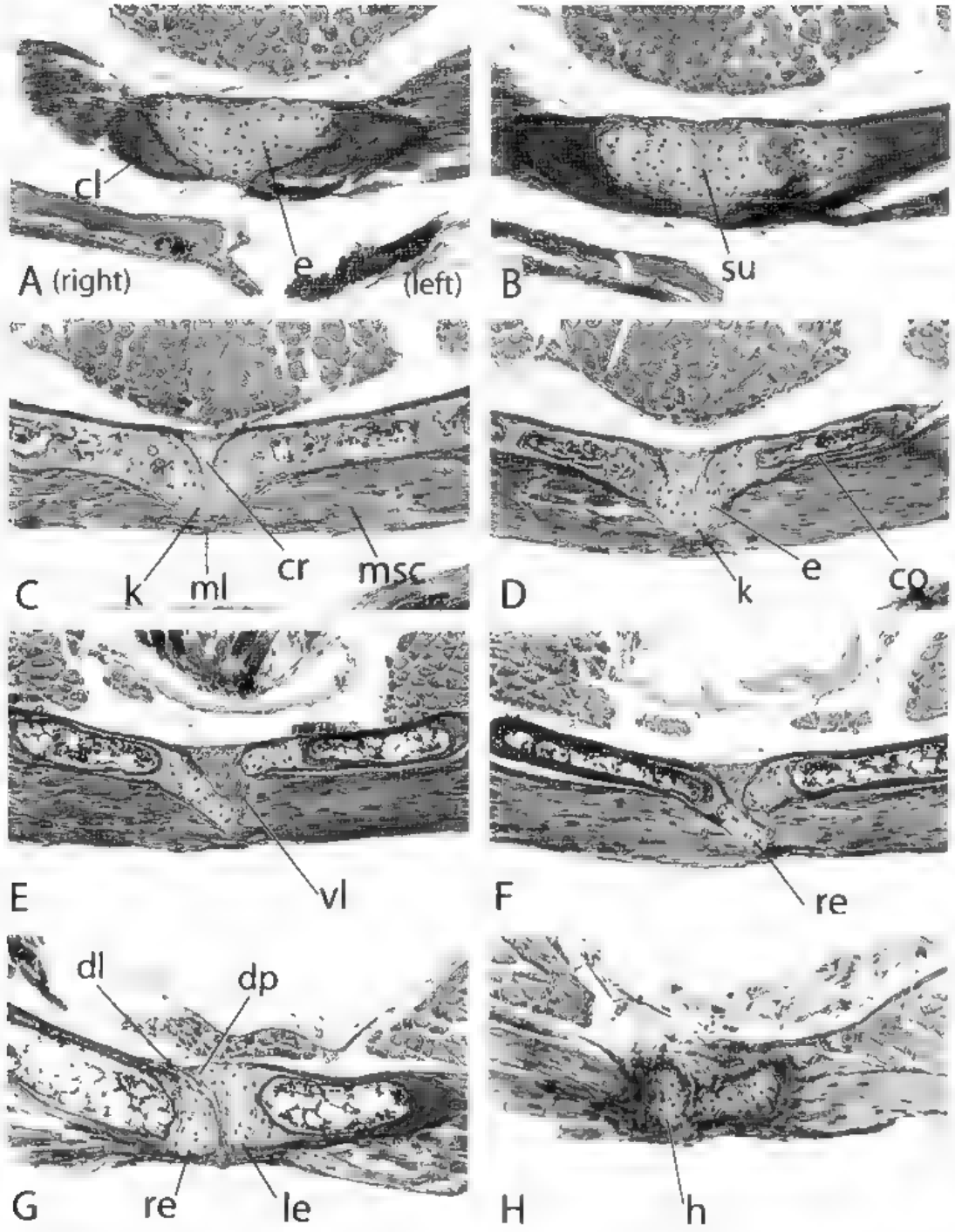


Fig. 3 — Histological cross sections, in an antero-posterior direction, of the ventromedial part of the pectoral girdle of an adult *Brachycephalus ephippium* (UMMZ 103568). The levels of the sections are indicated in fig. 2. cl, clavicle; co, coracoid; cr, crevice; dl, dorsal ligament; e, epicoracoids; h, epicoracoid horn; k, ventral keel; le, left epicoracoid; msc, *m. supracoracoideus*; re, right epicoracoid; su, suture; vl, ventral ligament.

by dense, regular connective tissue termed the ventral ligament (vl) The *m. supracoracoideus* inserts on the ventral ligament. Posteriorly (fig 3F), the right epicoracoid (re) slightly overlaps the left epicoracoid (le). The left epicoracoid abuts against the dorsomedial surface of the right epicoracoid At the midlevel of the coracoids (fig 3G), the left epicoracoid bears a small dorsal process (dp) that overlaps the right epicoracoid, a dorsal ligament (dl) joins this dorsal process to the dorsomedial surface of the right coracoid. Each epicoracoid terminates in a minute horn (h) (fig 3H) The *m sternoepicoracoideus* inserts on the posterior terminus of the horn.

RHINODERMA DARWINII

Anteriorly (fig. 2, 4A), the epicoracoids (e) are indistinguishably fused at the midline. The *m. supracoracoideus* (msc) inserts on the ventromedial surface of the clavicles, epicoracoids and medial ligament (ml). A small ventral keel (k) is present posteriorly (fig. 4B). The coracoids laterally flank the epicoracoids (fig 4C). An oblique suture (su) separates the epicoracoids (fig 4D) Posteriorly, a triangular notch (n) in the right side of the ventral keel is filled with loose connective tissue (fig. 4E); the *m. supracoracoideus* inserts on this connective tissue, the ventral surfaces of the right epicoracoid and the medial ligament. At the level of the coracoids (fig. 4F), the loose connective tissue in the notch is replaced by cartilage (x). Posteriorly (fig 4G), each epicoracoid terminates in a horn (rh) that curves posterolaterally. The horns and the sternum (s) are separated by sutures. Posteriorly (fig. 4H), the *m sternoepicoracoideus* (mse) inserts on the posterior ends of the epicoracoid horns.

INSUETOPHRYNUS ACARPICUS

The anterior epicoracoids are indistinguishably fused to one another at the midline (fig. 2, 5A), but slightly posteriorly (fig. 5B) the epicoracoids can be distinguished from one another, each bears a dorsomedial protuberance (dp) There is a distinct dorsomedial crevice and a rounded, ventromedial keel (k). *Muscle 1* (m1) inserts on the lateral surface of each epicoracoid and *Muscle 2* (m2) on the ventrolateral surface and medial ligament (ml) The dorsal crevice is extended ventrally as a sigmoid shape, the dorsal part of the left epicoracoid slightly overlaps the right epicoracoid (fig. 5C). *Muscle 3* (m3) inserts on the ventral part of the medial ligament. In the anterior region of the coracoid fenestra (fig 5D), the epicoracoids are free; the medial end of the left epicoracoid (le) is wide, and overlaps the right epicoracoid (re) The left side of the ventral keel is replaced by dense, regular connective tissue, the ventral ligament (vl), on which *muscle 2* inserts. Posteriorly (fig 5E), the left epicoracoid is triangular in section and the right epicoracoid elliptical. The right epicoracoid abuts against the ventral ligament and dorsal ligament (dl) extends between the medial end of the left epicoracoid and the right epicoracoid *Muscle 2* inserts on the ventral ligament and the lateral surface of each epicoracoid *Muscle 3* inserts mostly on the medial ligament. At the level of the coracoids (fig. 5F), a gap separates the medial ligament (ml) and the right epicoracoid (re), which overlaps the left extensively The epicoracoids terminate in a pair of horns (fig. 5G), each of which lies in a lateral sternal groove (sg). Parts of the horns are fused to the sternum A laterally directed ligament (ll) inserts on the posterior tips of the epicoracoid horns (fig. 5H); a *m sternoepicoracoideus* is not evident

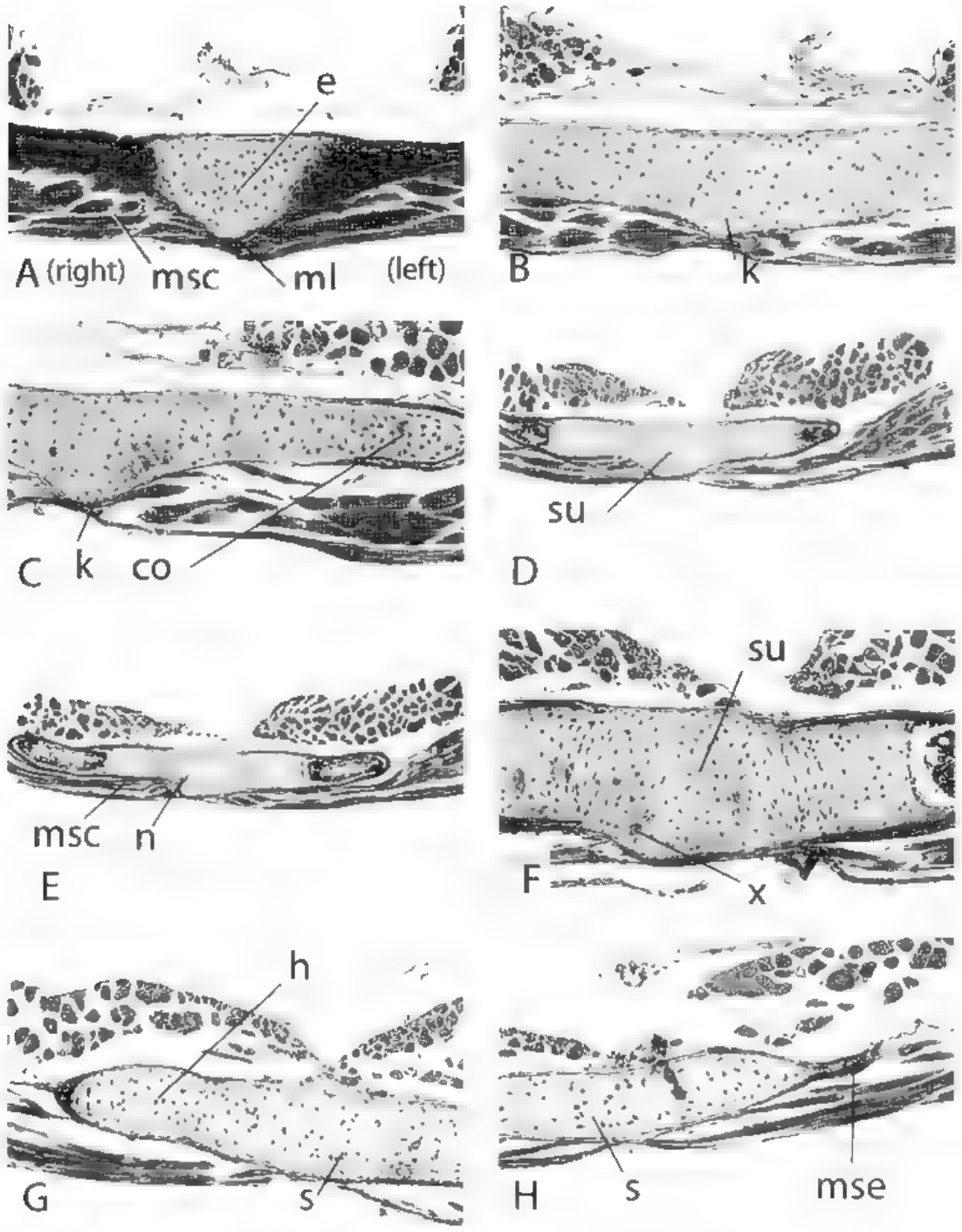


Fig. 4 — Histological cross sections, in an antero-posterior direction, of the ventromedial part of the pectoral girdle of *Rhinoderma darwinii* (UMMZ 143361). The levels of the sections are indicated in fig. 2. co, coracoid; e, epicoracoids; h, epicoracoid horn; k, keel; ml, medial ligament; msc, *m. supracoracoideus*; mse, *m. sternoepicoracoideus*; n, notch at the right side of the ventral keel; s, sternum; su, suture; x, part of the ventral keel replaced by cartilage.

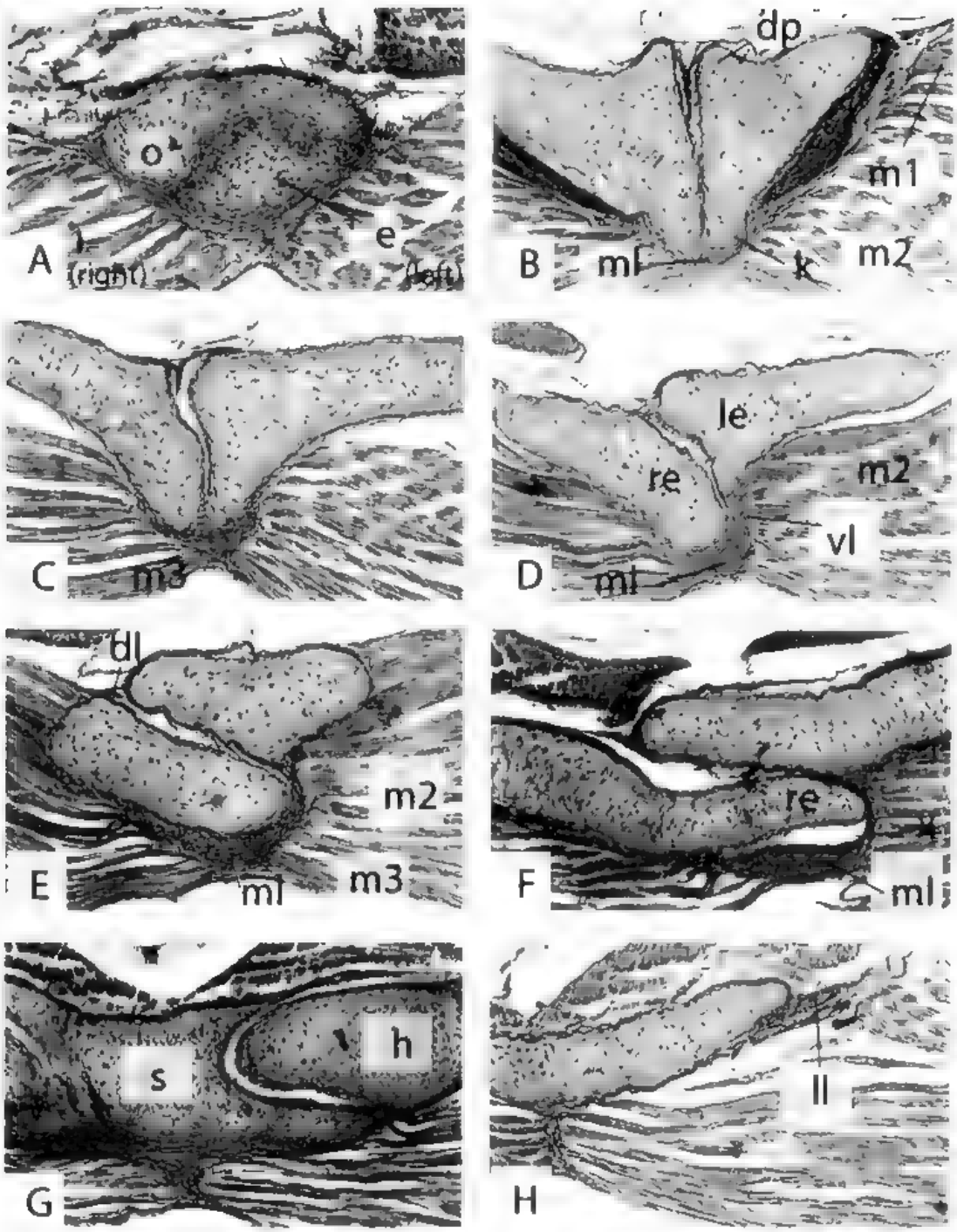


Fig. 5. Histological cross section in an antero-posterior direction, of the ventromedial part of the pectoral girdle of *Insulatophrynus arpiarus* (UMMZ 225142). The levels of the sections are indicated in fig. 2. dl, dorsal ligament; dp, dorsal protuberances; e, epicoracoids; h, epicoracoid horns; k, keel; le, left epicoracoid; ll, lateral ligament; m1, *muscle 1*; m2, *muscle 2*; m3, *muscle 3*; ml, medial ligament; o, omosternum; re, right epicoracoid; s, sternum; vl, ventral ligament.

GEOBATRACHUS WALKERI

Anteriomedially (fig. 2, 6A), the epicoracoids (e) are indistinguishably fused to one another. *Muscle 1* (m1) inserts on the lateral and ventral surfaces of the epicoracoids and on the medial ligament (ml). Posterior to the procoracoids (fig. 6B), the fused epicoracoids bear a shallow dorsomedial depression. Slightly posteriorly (fig 6C), the coracoids (co) lie lateral to the epicoracoids, which are separated by a suture (su) marked by a shallow dorsomedial depression. *Muscle 1* is divided into a wide slip, *muscle 1a* (m1a) that inserts on the coracoids, and a thin slip, *muscle 1b* (m1b) that inserts on the medial ligament. At the level of the coracoid shafts (fig. 6D), an ovoid ventral keel (k) is evident. The epicoracoids bear a shallow dorsomedial crevice; only *muscle 1b* is evident Slightly posteriorly (fig. 6E), only the ventral keel remains. The medial parts of the coracoids are replaced by a membrane (me). *Muscle 1b* inserts on the lateral and dorsolateral surfaces of the keel and on the medial ligament. Posteriorly (fig 6F), the epicoracoids and medial part of the coracoids are evident and the ventral keel is small. Posteriorly (fig. 6G), the epicoracoids diverge slightly from one another, and *muscle 3* (m3) inserts on their dorsal surfaces. At the posterior terminus (fig 6H), the epicoracoids and sternum are indistinguishably fused; neither epicoracoid horns nor the *m. sternoepicoracoideus* is evident.

ATELOPUS SUBORNATUS

Anteromedially (fig. 7A-B), the epicoracoids (e) are indistinguishably fused to one another. Posteriorly (fig. 7C), a small, triangular ventral keel (k) is evident. At the anterior level of the coracoids (fig. 7D), the fused epicoracoids are oval in cross section and the *m supracoracoideus* (msc) inserts on the medial ligament (ml) and ventrolateral surfaces of the epicoracoids, the *m coracoradialis* (mcr) on their dorsolateral and dorsal surfaces. Posteriorly (fig 7E), the coracoids laterally flank the epicoracoids, which are represented by two ovoid elements that are fused medially. The *m. rectus abdominis* (mra) inserts on the dorsomedial surfaces of the epicoracoids. At the posterior level of the coracoids (fig 7F), the epicoracoid horns (h) diverge from one another The horns are fused partially to the sternum (s) and sternal grooves are evident. The *m. sternoepicoracoideus* is absent.

OSORNOPHRYNE BUFONIFORMIS

Anteromedially (fig. 8, 9A-B), the epicoracoids (e) are indistinguishably fused to one another Slightly posteriorly (fig 9C), a suture (su) separates the epicoracoids and a small, triangular ventral keel (k) is evident *Muscle 1* (m1) inserts on the ventral surface of each clavicle (cl) and the medial ligament (ml). Posteriorly (fig. 9D), the epicoracoids bear a shallow, dorsomedial crevice and a rounded ventromedial keel *Muscle 1* inserts on the ventromedial surfaces of the procoracoids, lateral surfaces of epicoracoids and medial ligament. At the level of the coracoid fenestra (fig 9E), the epicoracoids are expanded (i e. bladelike), flat, and slightly curved *Muscle 1* inserts on the ventral surfaces of the epicoracoids and medial ligament An oblique suture (su) separates the two epicoracoids such that the left epicoracoid bears the ventral keel Between the coracoids (fig 9F), the epicoracoids

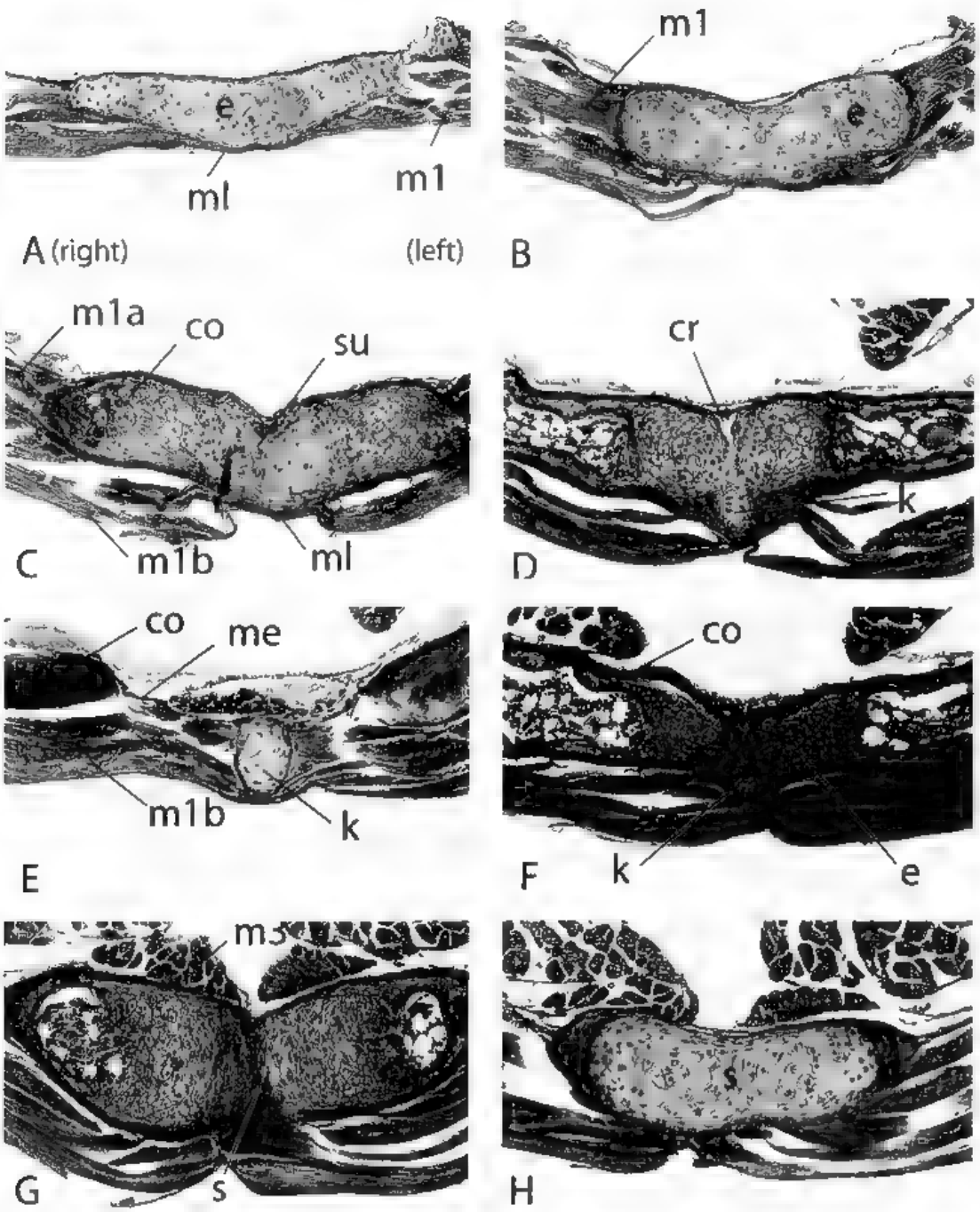


Fig 6 Histological cross section, in an antero-posterior direction, of the ventromedial part of the pectoral girdle of *Geobatrachus walkeri* (ICN 35.86) The levels of the sections are indicated in fig 2 co, coracoid, cr, crevice, e, epicoracoids, k, keel, m1, *muscle 1*, m1a, *muscle 1a*, m1b, *muscle 1b*, me, membrane; ml, medial ligament; s, sternum; su, suture.

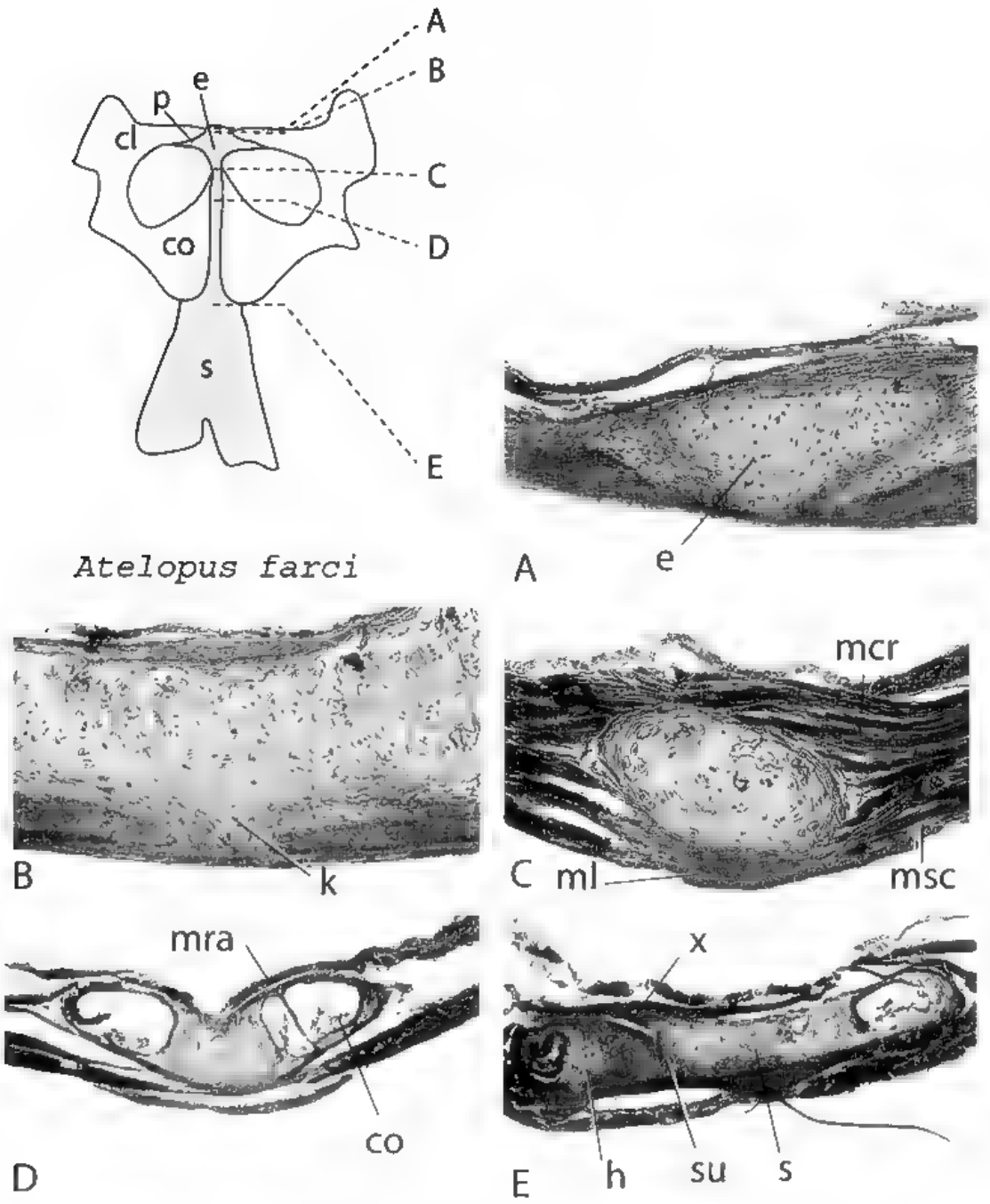
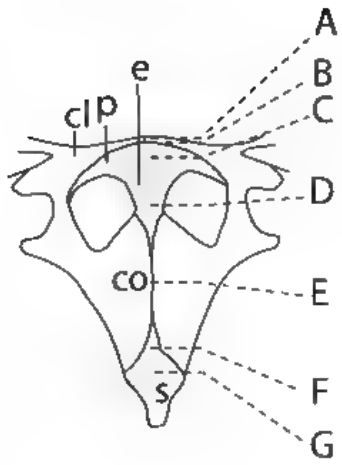
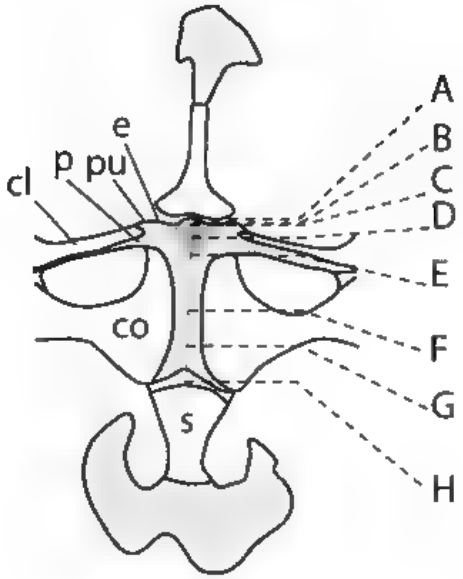


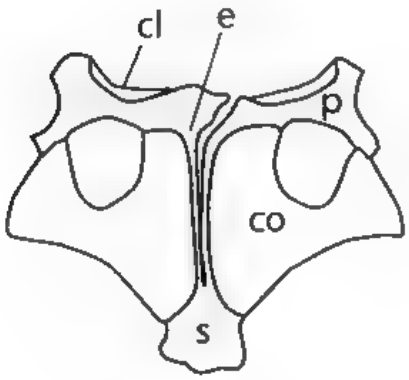
Fig. 7 Ventral view of the pectoral girdle of *Atelopus farci* (adapted from KAPLAN, 1994) and histological cross sections, in an antero-posterior direction, of the ventromedial part of the pectoral girdle of *Atelopus subornatus* (ICN 15820). cl, clavicle, co, coracoid, e, epicoracoid, h, epicoracoid horns, k, keel, mra, *m. rectus abdominis*, mcr, *m. coracoradialis*, ml, medial ligament, msc, *m. supracoracoideus*; p, procoracoids; s, sternum, su, suture, x, gap. Gray: cartilage, white: bone. A-E: corresponding transverse sections of drawing and photos.



Osornophryne bufoniformis



Rana sylvatica



Atopophrynus syntomopus

Fig. 8 Ventral view of the pectoral girdle of *Osornophryne bufoniformis* (adapted from RUIZ-CARRANZA & HERNANDEZ CAMACHO, 1976), *Rana sylvatica* (adapted from TYSON, 1987) and *Atopophrynus syntomopus* (adapted from MYERS & FORD, 1986) cl, clavicle, co, coracoid, e, epicoracoid, p, procoracoid, pu, *processus uncinatus*, s, sternum. Light gray: cartilage, dark gray: loose connective tissue; white: bone. A-H: transverse sections corresponding to those of fig. 9-10

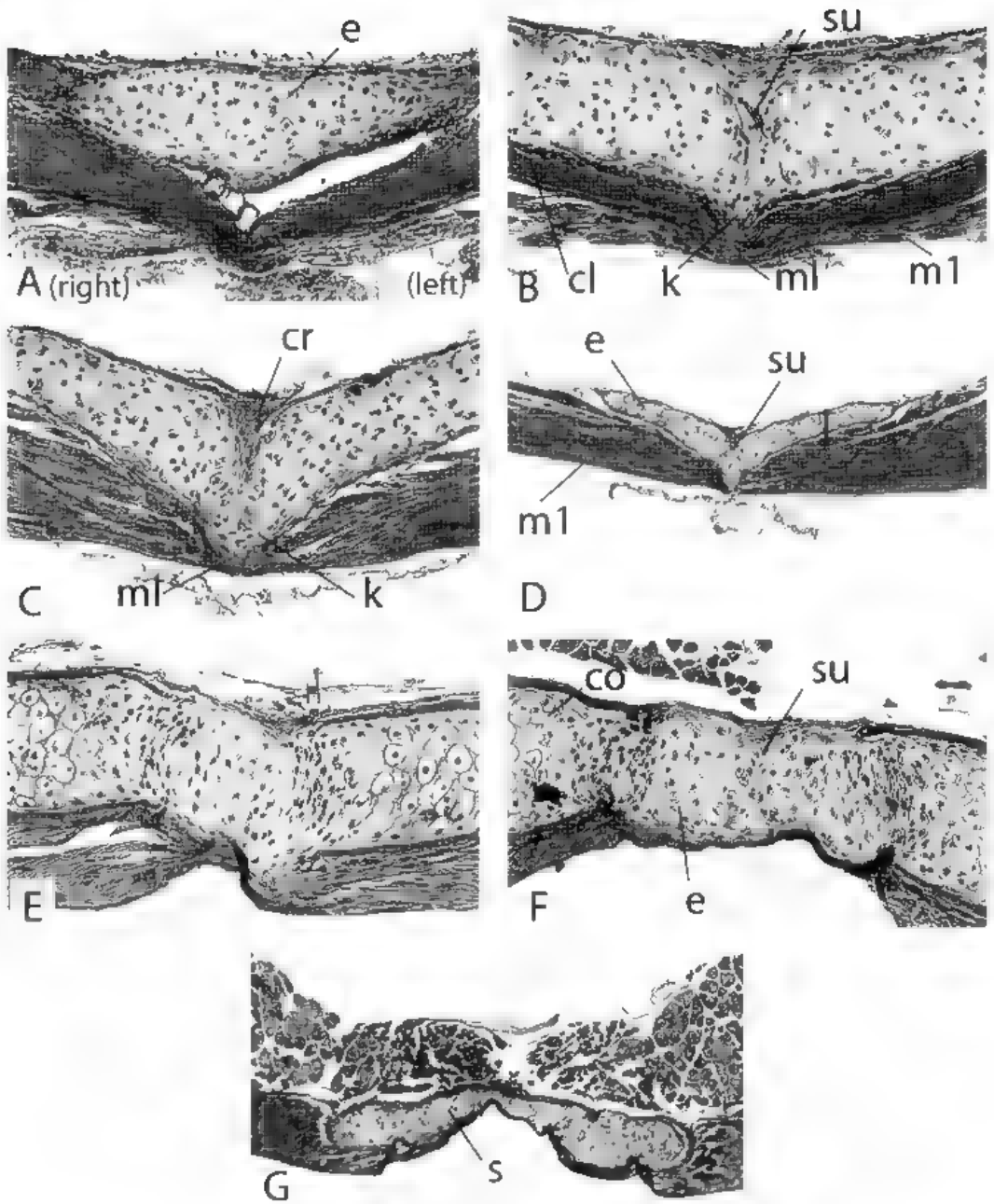


Fig. 9 Histological cross sections, in an antero posterior direction, of the ventromedial part of the pectoral girdle of *Osornophryne bufoniformis* (ICN 11505). The levels of the sections are indicated in fig. 8. co, coracoid, cl, clavicle, e, epicoracoid, cr, crevice, k, keel, m1, *muscle 1*, ml, medial ligament, s, sternum; su, suture

are indistinguishably fused and lack both, a ventral keel and dorsal crevice. Posteriorly (fig. 9G), a suture separates the epicoracoids. At the level of the sternum (fig. 9H), the epicoracoids are indistinguishably fused to this structure. Neither epicoracoid horns nor the *m. sternoepicoracoideus* are present.

RANA SYLVATICA

Anteriorly (fig. 8, 10A), the ventral keel of the epicoracoids bears a process (kp) that lies in the biforated base of the omosternum (o). Slightly posteriorly (fig. 10B), the anterior protuberance (pu) of each epicoracoid (i.e., *processus uncinatus*: FUSCH, 1926) laterally flanks the omosternum. In posterior sections (fig. 10C), the keel process is joined with the *processus uncinatus*. Near the anterior levels of the coracoid fenestra (fig. 10D), the epicoracoids bear a dorsomedial crevice (cr). The *m. supracoracoideus* (msc) inserts on the ventral keel and the *m. coracoradialis* (mcr) on the ventral surfaces of the clavicles. Posterior to the procoracoids (fig. 10E), the coracoids (co) flank laterally the epicoracoids and the epicoracoids are fused ventrally. The *m. coracoradialis* inserts on the lateral surface of each coracoid. At the midlevel of the coracoids (fig. 10F), the epicoracoids are surrounded by bone and, except medially and ventrally, they are eroded; the ventral keel (k) remains cartilaginous. Posteriorly (fig. 10G), a suture (su) separates the ventral keel and the epicoracoids. Posteriorly (fig. 10H), the ventral keel is replaced by the sternum (s) which is united synchondrotically with the keel. The posterior termini of the epicoracoids diverge as horns (h), which are surrounded by bone and fused to the dorsolateral parts of the sternum and to one another by a dorsal osseous bridge.

HYMENOCHIRUS BOETTGERI

Anteromedially (fig. 11A-B), the epicoracoids (e) are indistinguishably fused to one another. At the anterior level of the coracoid fenestra (fig. 11C), the epicoracoids are wide, flat and expanded in cross section. The *m. coracoradialis* (mcr) inserts on the lateral and ventrolateral surfaces of the epicoracoids. At the midlevel of the coracoid fenestra (fig. 11D), the epicoracoids are narrower. Posterior to the coracoids (fig. 11E), the epicoracoids diverge laterally as two epicoracoid horns. These horns have densely packed chondrocytes and are fused to the sternum (s). The *m. sternoepicoracoideus* is absent.

FROSTIUS PERNAMBUCENSIS

Anteromedially (fig. 12A), the epicoracoids (e) are indistinguishably fused to one another. *Muscle 1* (m1) inserts on the ventromedial surface of each clavicle (cl). Posteriorly (fig. 12B), a suture separates the epicoracoids. Posterior to the procoracoids (fig. 12C), the epicoracoids are small and ovoid in sections and bear a dorsomedial depression. *Muscle 1* inserts on the lateral, dorsolateral and ventrolateral surfaces of the epicoracoids and medial ligament (ml). At the level of the coracoid (fig. 12D), the *m. rectus abdominis* (mra) inserts on the dorsomedial surface of the epicoracoids. Posteriorly (fig. 12E), the epicoracoids horns

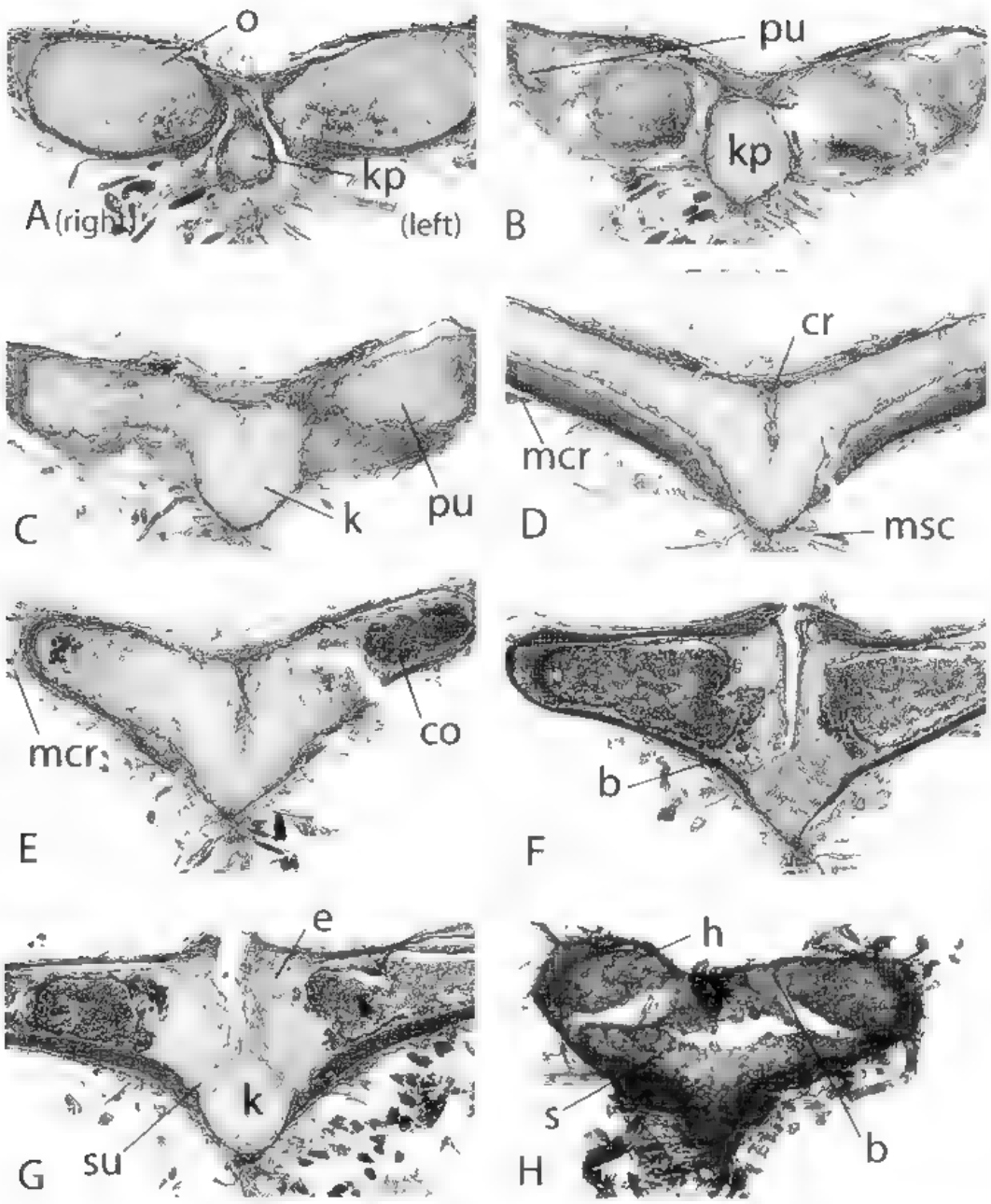


Fig. 10 Histological cross section, in an antero posterior direction, of the ventromedial part of the pectoral girdle of *Rana sylvatica* (UMMZ). The levels of the sections are indicated in fig. 8. b, bone, co, coracoid; cr, crevice, e, epicoracoid, h, epicoracoid horn, k, keel, kp, keel process, mcr, *m. coracoradialis*, msc, *m. supracoracoideus*; o, omosternum; pu, *processus uncinatus*; s, sternum, su, suture.

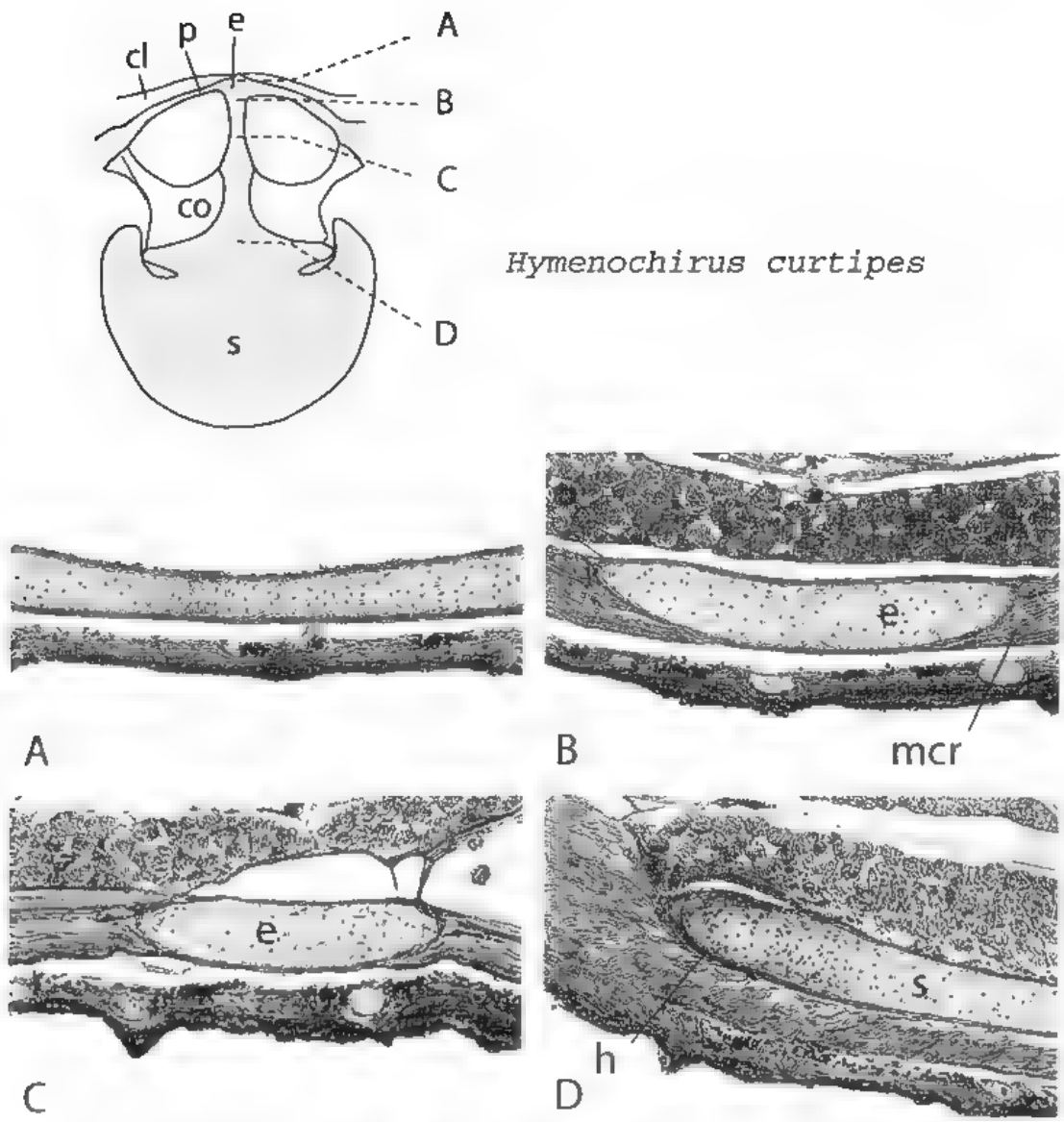


Fig. 11. Ventral view of the pectoral girdle of *Hymenochirus curtipes* (adapted from De Villiers, 1929) and histological cross section, in an antero-posterior direction, of the ventromedial part of the pectoral girdle of *Hymenochirus boettgeri* (UMMZ). cl, clavicle; co, coracoid; e, epicoracoid; h, epicoracoid horn; mcr, *m. coracoradialis*; p, procoracoid; s, sternum. Gray: cartilage; white: bone. A-D, corresponding cross sections of drawing and photos.

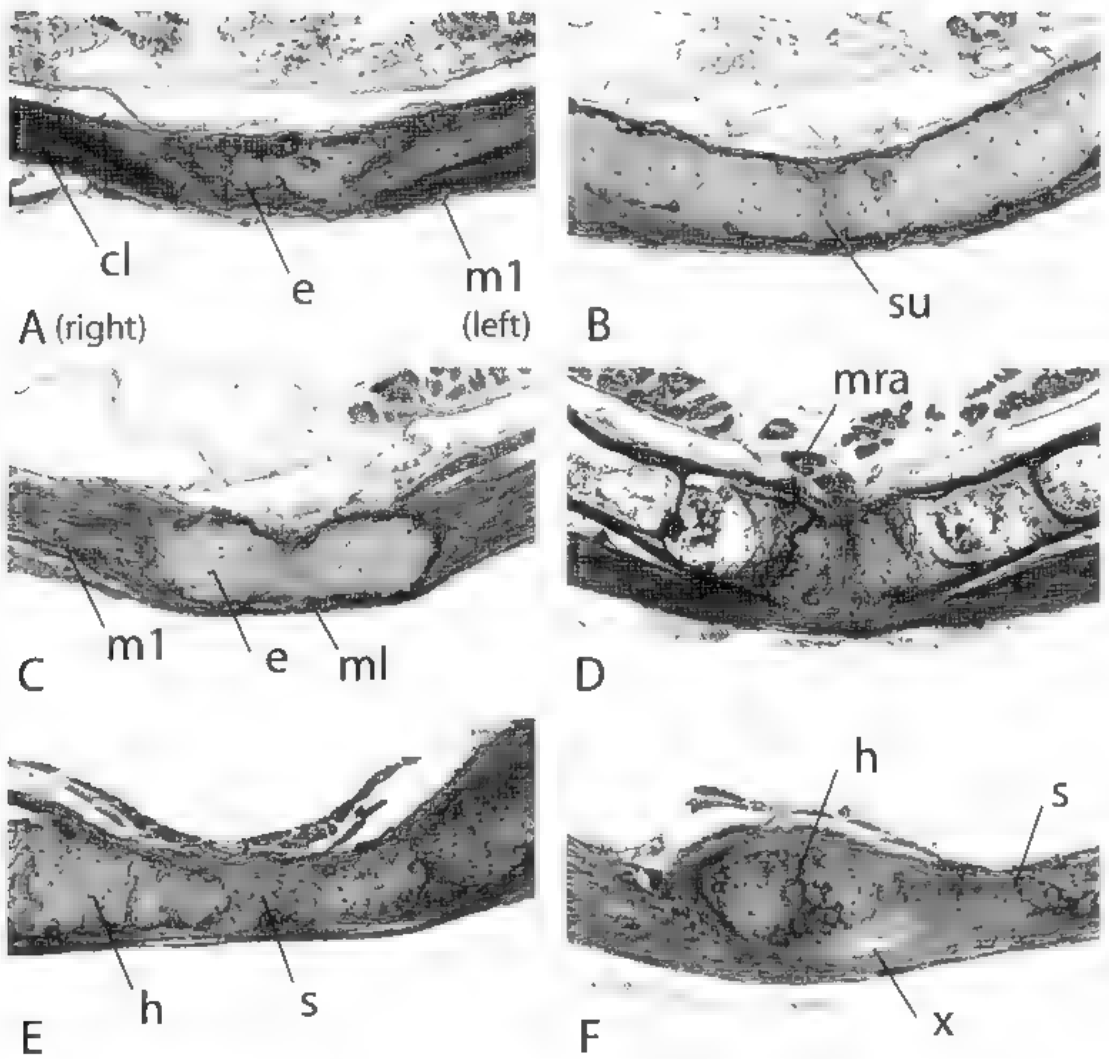


Fig. 12 — Histological cross section, in an antero-posterior direction, of the ventromedial part of the pectoral girdle of *Frostius permanbucensis* (UMMZ 225143). cl, clavicle, e, epicoracoid, h, epicoracoid horn, m1, *muscle 1*, mra, *m. rectus abdominis*, ml, medial ligament, s, sternum, su, suture, x, gap.

diverge from one another. The sternum and horns, which have different coloration and cell densities, are fused to one another. Posteriorly (fig. 12F), gaps separate the horns and sternum. The *m. sternoepicoracoideus* is absent.

DISCUSSION

Of the pectoral girdles studied, only those of *Atelopus subornatus*, *Frostius pernambucensis*, *Hymenochirus boettgeri*, *Osornophryne bufoniformis* and *Rana sylvatica* have completely fused, non-overlapping epicoracoids. However, the epicoracoids of each of these taxa, except *O. bufoniformis*, diverge slightly from one another posterior to the coracoids and, thus, are not fused throughout their entire lengths. The condition in *Atopophrynus* and *Pseudhymenochirus* is unknown. The epicoracoids of *Geobatrachus walkeri* are completely fused and not overlapping except for a small area at the level of the coracoid shafts. At this level, the structure of the epicoracoids and medial part of the coracoids is disorganized; this morphology is unique in anurans.

In *Rhinoderma darwinii*, the epicoracoids are indistinguishably fused and not overlapping anterior to the midlevel of the coracoid fenestra, but fused (i.e., through their overlapping surfaces, rather than the medial ends) and overlapping posterior to this level. GRIFFITHS (1957, 1963) considered the overlap of the epicoracoids to start posterior to the coracoids, whereas KAPLAN (1993) thought that it started at the posterior level of the procoracoids. The overlap of the epicoracoids is evident in froglets (stage 46) (KAPLAN, 1993), however, in sexually mature individuals, it is evidenced only by the presence of an oblique medial suture and a free (i.e., unfused) medial epicoracoid margin (fig. 2A-B). The girdle morphology in which the epicoracoids are fused and overlapping in the same cross section, and where the fused parts are their overlapping surfaces, rather than their medial ends, is unique in anurans.

In *Brachycephalus ephippium*, the epicoracoids are fused without overlap from their anterior tips to the posterior level of the coracoid fenestra, posterior to this level, they are free (i.e., attached by dense connective tissue) and overlapping. The girdle of *B. ephippium* is arciferofirmisternal (viz., epicoracoids fused to, and not overlapping, one another from their anterior tips to a level posterior to the clavicles and free, and overlapping, posteriorly to this point (DUELLMAN & TRUEB, 1985). However, the girdle of *B. ephippium* differs from other arciferofirmisternal girdles (e.g., *Dendrophryniscus*, *Melanophryniscus*) in having a very reduced area where the epicoracoids are free and overlapping.

TRUEB (1973) and FORD & CANNATELLA (1993) argued that *Brachycephalus* has completely ossified epicoracoids, this study shows that the epicoracoids are cartilaginous (i.e., by definition, the epicoracoids are the cartilaginous remnant of the embryonic coracoid-epicoracoid cartilage, FUSCH, 1926, TYSON, 1987; KAPLAN, 1993). TRUEB (1973) considered the epicoracoids to be juxtaposed, rather than fused, in *B. ephippium*. My results indicate that the epicoracoids are fused to one another up to the anterior level of the coracoids, and firmly attached to one another posterior to this level.

The girdle of *Insuetophrynus acarpicus* is arciferofirmisternal, because the non-overlapping epicoracoids are fused from their anterior tips to the posterior level of the procoracoids. They are unfused and overlapping posterior to this level.

The girdles of *Atelopus subornatus*, *Frostius pernambucensis*, *Hymenochirus boettgeri* and *Osornophryne bufoniformis* differ from those of *Rana sylvatica* and *Hoplobatrachus chinensis* (often referred to as *Rana rugulosa*, but see KOSUCH et al., 2001) (KAPLAN, 2000) by having the most anterior parts of the epicoracoids in contact with one another and indistinguishably fused. In *R. sylvatica* and *H. chinensis*, the anterior epicoracoids (i.e., the *processus uncinatus*, because the anterior process of the ventral keel is of sternal origin; KAPLAN, 1993) are free (i.e., attached by dense connective tissue) and diverging from one another. This observation is consistent with the hypothesis that pseudofirmisterny and firmisterny evolved independently, however, it is still unknown whether the girdle morphologies of *R. sylvatica* and *H. chinensis* are widespread among Ranoidea. The characteristic girdle morphology known long ago in *Hoplobatrachus* and related groups (BOLKAY, 1915) and referred to as "arcizony" (DECKERT, 1938) or "arciferal-like condition" (TRUEB, 1973: 95) is a variant of firmisterny and has nothing to do with pseudofirmisterny.

The girdles of *Atelopus subornatus* and *Hymenochirus boettgeri* differ from those of *Frostius pernambucensis* and *Osornophryne bufoniformis* by having the epicoracoids indistinguishably fused. DE VILLIERS (1929) incorrectly stated that in *Hymenochirus* the epicoracoids are separated by a suture. In *F. pernambucensis* and *O. bufoniformis*, the epicoracoids are indistinguishably fused to one another from their anterior tips to the posterior level of the procoracoids and separated by a suture posterior to this level. These differences are minimal, and it is still unknown whether the presence or absence of suture between the epicoracoids is the result of ontogenetic and/or intraspecific variation. Therefore, the structural homology of the girdles of *A. subornatus*, *F. pernambucensis*, *H. boettgeri* and *O. bufoniformis* is equivocal.

I found several morphological differences among the girdles of the non-ranoid frogs studied. The epicoracoids are expanded and flat in *Hymenochirus boettgeri* and *Osornophryne bufoniformis*, but not expanded and ovoid in *Frostius pernambucensis* and *Atelopus subornatus*. No muscle inserts on the dorsal and lateral surfaces of the epicoracoids in *O. bufoniformis*, but they do on the lateral and dorsal surfaces in *A. subornatus* and *F. pernambucensis* and in the lateral surfaces in *H. boettgeri*. In *O. bufoniformis*, a suture separates the epicoracoids asymmetrically whereas this separation is symmetrical in *F. pernambucensis*. The systematic value of these characters is unknown.

The hypothesis that pseudofirmisterny is a synapomorphy uniting *Brachycephalus* and *Atelopus* (GRIFFITHS, 1963) and *Brachycephalus* and *Psyllophryne* (FORD & CANNATELLA, 1993) is false because *B. ephippium* lacks this character. Similarly, pseudofirmisterny does not support the monophyly of *Geobatrachus* and *Atopophrynus* because *Geobatrachus* lacks this character. Moreover, the girdles of these two taxa differ externally, as is evident by comparison of figures 2 and 8.

The character "epicoracoids completely fused to, and not overlapping, one another" unites only *Atelopus*, *Frostius* and *Osornophryne*. However, there are morphological differences among their girdles (e.g., epicoracoids indistinguishably fused or partially separated by a suture, symmetrically or asymmetrically separated by a suture, expanded or not expanded) that may be phylogenetically informative.

RESUMEN

Se estudiaron histologicamente las cinturas pectorales de las siguientes especies: *Atelopus subornatus*, *Brachycephalus ephippium*, *Frostius pernambucensis*, *Geobatrachus walkeri*, *Hymenochirus boettgeri*, *Insuetophrynus acarpicus*, *Osornophryne bufoniformis*, *Rana sylvatica*, *Rhinoderma darwinii*. Dentro de los anuros no ranoideos estudiados, solamente *A. subornatus*, *F. permanbucensis*, *H. boettgeri* y *O. bufoniformis* presentan los cartilagos epicoracoidales completamente fusionados y sin sobrelaparse (i e., pseudofirmisternia). Las cinturas pectorales de *G. walkeri* y *R. darwinii* son unicas dentro de los anuros. Las cinturas pectorales de *B. ephippium* y *I. acarpicus* son arciferofirmisternales. Las diferencias morfologicas entre las cinturas pectorales firmisternales y pseudofirmisternales sugieren que estas no son homologas.

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Corresponding editor: Alain DUBOIS.